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Combining simplicity and functionality: mouthpart sensilla in the miniature parasitoid wasp *Megaphragma viggianii* (Hymenoptera, Trichogrammatidae)

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Abstract

Insects depend on complex sensory systems to detect food sources, locate mates, and navigate in the environment. In the smallest insects, miniaturization imposes major constraints on anatomy and physiology, but it remains poorly understood how this affects the structure and function of sensory systems, such as the sensilla on the mouthparts. The specific problem addressed in this study is how extreme miniaturization influences the diversity, distribution, and structural complexity of mouthpart sensilla in the minute parasitoid wasp *Megaphragma viggianii* Fusu, Polaszek & Polilov. Using scanning and volumetric electron microscopy, we show that despite its minute body length of 0.2–0.3 mm, *M. viggianii* possesses a set of 70 sensilla on its mouthparts, including four major types (chaetoid, basiconic, coeloconic, and campaniform). These wasps display no noticeable sexual dimorphism in the structure and distribution of their mouthpart sensilla, and the set of sensilla is generally identical in different individuals. Compared to larger Hymenoptera, *M. viggianii* exhibits a reduced number of sensilla, but maintains the same types of sensilla and their similar position, suggesting stable developmental and functional traits. These findings confirm that miniaturization does not reduce the diversity of the sensilla, but instead drives simplification at the structural level, while preserving their functional roles. These insights not only advance our understanding of insect sensory biology but also contribute to elucidating broader questions of evolutionary morphology and functional scaling of biological systems.

Keywords

Megaphragma, miniaturization, mouthparts, sensilla, Trichogrammatidae

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Introduction

The sensory system plays an important role in the lives of insects, being a source of information about their surroundings and the state of their own bodies. It is used to search for food and for sexual partners and as to perform spatial orientation and movement coordination (Kamikouchi et al. 2009). The sensory systems of insects possess a variety of sensory organs including sensilla. These are modified cuticular hairs that have at least one bipolar neuron and, usually, several auxiliary cells. Sensilla are located over the entire surface of the insect body, but are most numerous on the antenna, mouthparts, legs, wings, and genitalia (Chapman 1969). Insect sensilla have various modalities and can be mechano-, chemo-, thermo- and hygroreceptors (Ivanov 2000).

Various classifications of sensilla have been proposed depending on their structure. Snodgrass (1926) classified sensilla based on the morphology of their cuticular part: hair, plate, campaniform, and scolopophorous organs. Hair organs are further divided into sensilla trichodea, sensilla chaetica, sensilla basiconica, sensilla coeloconica, sensilla ampullacea, and sensilla squamiformia. According to Altner and Prillinger (1980), sensilla are divided into aporous, uniporous and multiporous (single- or double-walled). Aporous sensilla can perform a mechano-, hygro-, or thermoreceptor function; uniporous sensilla can be mechanoreceptors or contact chemoreceptors; multiporous sensilla can contain chemo-, thermo-, and hygroreceptor cells. It was also proposed to divide chemoreceptor sensilla into thin-walled (olfactory chemoreceptors) and thick-walled (contact chemoreceptors) (Slifer 1970).

Miniaturization is one of the key trends in insect evolution, which in some cases leads to an extreme decrease in body size, making it comparable to that of unicellular organisms. Such a change in body size inevitably leads to a significant restructuring of all systems and organs of insects, including modifications at the cellular level (Polilov 2015, 2016; Minelli and Fusco 2019). Changes also affect the sensory system of miniature insects, making it interesting in terms of the peculiar optimization of the structure of sensory organs and their distribution on the body surface.

Although sensory organs of many insects have been previously studied in detail (Mazokhin-Porshnyakov et al. 1983; Zacharuk and Shields 1991; Hallberg and Hansson 1999; Ivanov 2000; Missbach et al. 2014; van der Kooi et al. 2021), studies on the scaling of insect sensory system began to appear relatively recently, and there are few publications on this subject. The available studies mostly focus on the antennae and eyes of some insects. Research in this area shows that the body size of insects significantly affects the structure and quantitative characteristics of compound eye, as well as antenna and antennal sensilla both on the interspecific (Symonds and Elgar 2013; Ramirez Esquivel 2017; Godfrey et al. 2021) and on the intraspecific level (Smallegange et al. 2008; Ramirez Esquivel et al. 2014; van der Woude and Smid 2016). Some review articles on the scaling of insect eyes (Makarova et al. 2022a) and sensilla (Makarova et al. 2022b) have been published recently. Both antennae and eyes have a tendency to decrease the number of functional units (sensilla or ommatidia) during miniaturization.

For example, in the miniature wasp *Trichogramma evanescens* Westwood, the length of the ommatidium and rhabdom decreases, the processes of the pigment cells lose contact with the basement membrane, and average pigment granule volume is reduced (Fischer et al. 2011, 2019). The eyes of the smaller wasp *M. viggianii* Fusu, Polaszek & Polilov, 2022 contain several times fewer ommatidia than in *T. evanescens*, a difference probably functionally compensated by the larger lens diameter of the ommatidia and by their wider and shorter rhabdoms (Makarova et al. 2025). In general, smaller insects tend to have apposition eyes instead of superposition ones (Gokan and Meyer-Rochow 2000; Fischer et al. 2010; Makarova et al. 2015, 2019). This may be related to the fact that superposition is limited by the minimum size of the clear zone, the zone between the lens and retina (Gokan and Meyer-Rochow 2000; Meyer-Rochow and Gál 2004; Honkanen and Meyer-Rochow 2009). The number of ommatidia also correlates with body and head size, being higher in larger insects (Gokan and Meyer-Rochow 2000; Makarova et al. 2019).

Similarly, the number of antennal sensilla within the same species is often higher in larger insects, which was shown for the housefly *Musca domestica* L. (Smallegange et al. 2008) and for the *T. evanescens* (van der Woude and Smid 2016). Studies of the antennae of the *Megaphragma viggianii* (Diakova et al. 2018; Diakova and Polilov 2021) and the featherwing beetle *Scydosella musawasensis* Hall (Diakova and Polilov 2020) have shown that the number of sensilla on the antenna diminishes with decreasing body size, but the size of the sensilla themselves and the number of their types remain unchanged. The number of sensilla can vary considerably among wasps of different body sizes: depending on the species and sex, representatives of the genus *Megaphragma* Timberlake have 39–49 sensilla on their antennae, while the antennae of large parasitoid wasps can bear up to 9000 sensilla (Das et al. 2011). Miniature insects are also characterized by simplification of the structure of their sensilla: e.g., placoid sensilla without auxiliary cells have been found in *M. viggianii* (Diakova and Polilov 2021).

Megaphragma includes some of the smallest parasitoid wasps that parasitize the eggs of the thrips *Heliothrips haemorrhoidalis* (Bouché) (Bernardo and Viggiani 2002). Their body length is approximately 0.2 mm, and they have strongly reduced heart, tracheal system, and muscular system (Polilov 2017). Their extremely small size affects even the internal structure of neurons: they have anucleate neurons, not known in other organisms (Polilov 2012), except for miniature wasps of another genus, *Camptoptera* Foerster (Polilov et al. 2023). Despite the greatly simplified structure, *Megaphragma* females have a fairly complex behavior that allows them to detect host eggs, which indicates a fully functional sensory system.

Despite the growing interest in the miniaturization of insect sense organs, data on the structure of sense organs of the smallest insects and on their modifications related to miniaturization remain incomplete. In order to build a more complete picture, reflecting the principles of and limits to the miniaturization of insect sensory organs, data on their structure and location on mouthparts are required, which are provided in this study. The aim of this study is to continue the studies of the sensory organs of miniature insects and to reveal the patterns of miniaturization of mouthpart sensilla in *M. viggianii*.

Material and methods

This study is based on 41 adult males and 35 adult females of *Megaphragma viggianii*, (Hymenoptera: Trichogrammatidae) reared in the laboratory from eggs of *Heliothrips haemorrhoidalis* (Bouché, 1833). The material was fixed in 2% glutaraldehyde + 2% paraformaldehyde + 0.1% Triton + 0.1M phosphate-buffered saline solution for 20–24 hours and transferred to 70% ethanol. Then the material was dehydrated in 96% ethanol for 1 hour, in 100% ethanol for 30 minutes (two iterations) and in acetone for 15 minutes (two iterations). After dehydration it was dried in a Hitachi HCP-2 Critical Point Dryer. The dried specimens were mounted on scanning electron microscopy holders by using conductive tape and coated with a 20 nm layer of gold using a Cressington-208HR Ion Coater. Photographs of the mouthparts and individual sensilla were obtained using Jeol JSM-6380 and FEI Quattro S scanning electron microscopes. To obtain photographs of hidden medial sides of mouthparts, the heads of multiple insects were split into parts with entomological pins, then parts of the heads in water drops were put on the surface of glass pieces attached to scanning electron microscopy holders. After drying, the same coating method was applied to these specimens.

To obtain information on the ultrastructure of the sensilla types and to study the sensilla that are not visible from the surface, three-dimensional electron microscopy (vEM) was used. In this study we used images obtained earlier (Chua et al. 2023; Desyatirkina et al. 2023) by using the protocol described previously (Polilov et al. 2021).

The length and base width of the sensilla were measured in series of images with ImageJ 1.52a program. The obtained data were used to calculate the mean values of sensilla sizes and standard errors of the mean, as well as the minimum and maximum sizes of these structures. The measured lengths of the sensilla were used to carry out one-way Kruskal–Wallis ANOVA test with sex as the grouping variable and lengths of sensilla of every type as the dependent variables. The goal of this analysis was to determine whether *M. viggianii* has sexual dimorphism in sensillum length.

Results

Four types of sensilla were found on the mouthparts of males and females of *Megaphragma viggianii*:

Chaetoid sensilla (chs) are the most numerous type of sensilla on the mouthparts of *M. viggianii*. These are elongated, slightly curved or straight structures, with slight striation or without it (Fig. 3A, B). They also have sockets with edges slightly elevated above the surface of the cuticle. The width of chaetoid sensilla gradually decreases from the base to the tip; the tips are usually rounded. The length of these sensilla varies depending on their position on the mouthparts (Table 1). Most chaetoid sensilla are innervated by a single neuron and have no auxiliary cells (Fig. 4A, D). The dendrite of the neuron ends near the base of these sensilla and has a prominent tubular body.

Table 1. Average sizes of sensilla with different positions on *M. viggianii* mouthparts, μm.

Position	Length	Width
md-chs-1	3.9 ± 0.17	0.66 ± 0.014
md-chs-2	7.8 ± 0.33	0.64 ± 0.013
md-chs-3	4.3 ± 0.15	0.59 ± 0.008
md-chs-4	10.6 ± 0.25	0.72 ± 0.012
md-cos-1	1.0 ± 0.05	0.34 ± 0.014
md-cos-2	0.9 ± 0.03	0.34 ± 0.013
mx-chs-1	11.9 ± 0.41	0.70 ± 0.011
mx-chs-2	5.0 ± 0.2	0.53 ± 0.013
mx-chs-3	4.4 ± 0.12	0.57 ± 0.019
mxp-chs	13.4 ± 0.28	0.85 ± 0.011
mxp-bcs	5.0 ± 0.1	0.92 ± 0.014
lab-chs-1	12.1 ± 0.43	0.67 ± 0.011
lbp-chs-1	11.0 ± 0.25	0.81 ± 0.009
lbp-chs-2	2.8 ± 0.09	0.64 ± 0.014

On the distal parts of the maxilla, there is a non-innervated subtype of chaetoid sensilla, which lacks either dendrites or auxiliary cells (Figs 3C, 4B). These structures are thicker than innervated chaetoid sensilla and resemble spikes.

Coeloconic sensilla (cos; Fig. 3D) are partially submerged into a deep cuticular pocket. Their external part is slightly flattened, while their submerged part has a round cross-section. The surface of these sensilla is smooth and has no visible pores or grooves; their tips are rounded. They are innervated by one dendrite without a tubular body and have no auxiliary cells (Fig. 4E). The length of the visible part of these sensilla is 1.00 ± 0.05 μm.

Basiconic sensilla (bcs) are peg-like structures that are usually shorter than chaetoid sensilla. Two subtypes of these sensilla were found on the mouthparts of *M. viggianii*.

Porous basiconic sensilla (Fig. 3E) can be observed on the maxillary palp. Their shape resembles a stick with a rounded tip. The surface of the sensilla is covered with visible pores that are numerous on the tip of the sensilla, sometimes occur on their lateral side and are almost absent near their base. The bases of the sensilla have sockets with a smooth cuticular ridge. The sensilla have six dendrites entering the sensillar processes (Fig. 4C). Some of the dendrites reach the tip of the sensillum, others end in the middle. The length of the sensilla is 5.0 ± 0.15 μm.

Aporous basiconic sensilla (Fig. 3F) are positioned on the tip of the labium. These sensilla have smooth sockets and a conical shape: their width gradually decreases from the base to the tip. Their surface has no visible pores. The sensilla are innervated by three dendrites that reach at least the middle of the processes of the sensilla (Fig. 4D). One of the dendrites has a tubular body.

Campaniform sensilla (cfs) are completely submerged below the cuticle and not visible from the surface (Fig. 4F). These sensilla are comprised of a single dendrite with a tubular body and a socket septum which attaches the dendrite to the cuticle.

Distribution of the sensilla

Distribution of the sensilla is identical in males and females. The sensilla set is generally stable, but shows very rare aberrations in some individuals. The normal set of sensilla is shown in Figs 1, 2. The numbers of different sensilla on the mouthparts are given in Table 2.

A mandible (Figs 2A, B, 5A, B) has three chaetoid and two coeloconic sensilla on the lateral surface and four chaetoid sensilla on the medial surface. Chaetoid sensilla on the lateral surface are arranged in a row extending from the proximal to the distal part of the mandible. The tips of the chaetoid sensilla are pointing in the medial and distal directions. One of the chaetoid sensilla on the medial surface is close to the ventral margin of the mandible and is visible from the outside, its tip pointing distally. The

Table 2. Number of sensilla of each type on *M. viggianii* mouthparts.

Mouthparts	chs	cfs	bcs	cos
Mandibles (both)	14	20	0	4
Maxillae (both)	20	0	2	0
Labium	8	0	2	0

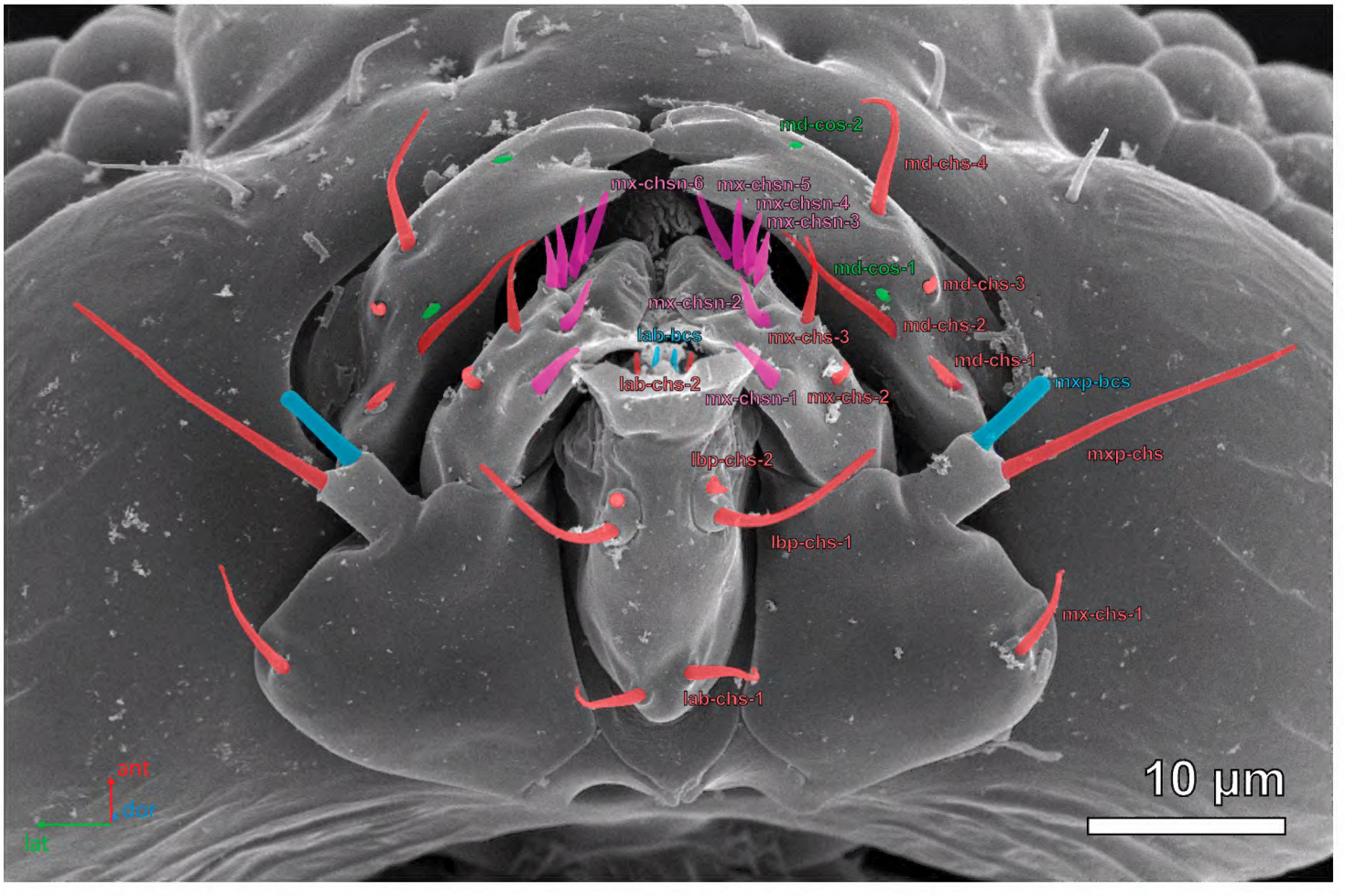

Figure 1. Map of mouthpart sensilla distribution in *M. viggianii*, with sensilla codes. Image of male mouthparts is given as an example; females show the same distribution of sensilla. Abbreviations: md – mandible; mx – maxilla; mxp – maxillary palp; lab – labia; lbp – labial palp; chs – chaetoid sensilla; chsn – non-innervated chaetoid sensilla; cos – coeloconic sensilla; bcs – basiconic sensilla; ant – anterior direction; dor – dorsal direction; lat – lateral direction.

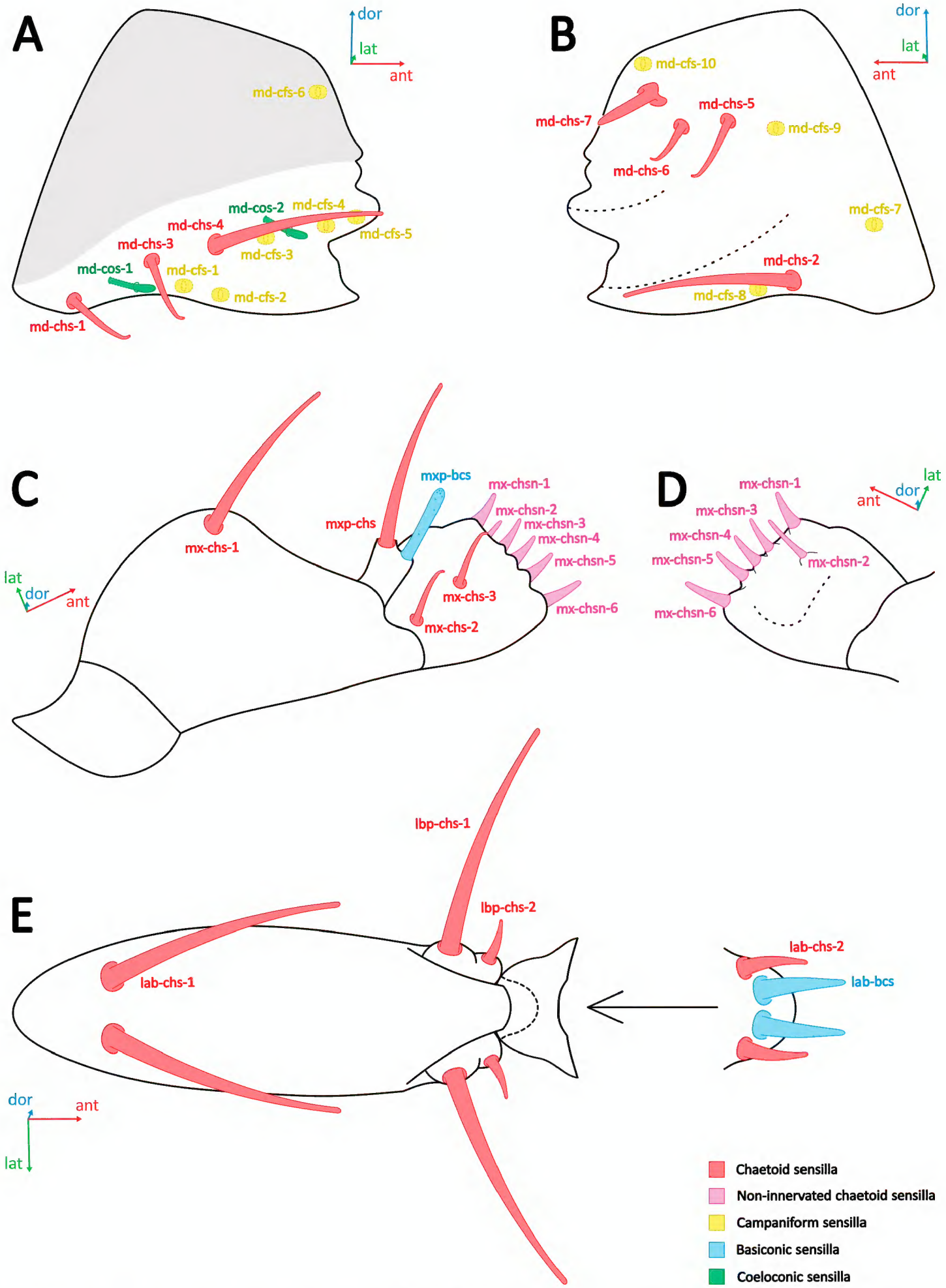

Figure 2. Schemes showing the position of sensilla on *M. viggianii* mouthparts. **A** lateral surface of mandible **B** medial surface of mandible **C** lateral surface of maxilla **D** medial surface of maxilla **E** ventral surface of labium. Abbreviations: md – mandible; mx – maxilla; mxp – maxillary palp; lab – labia; lbp – labial palp; chs – chaetoid sensilla; chsn – non-innervated chaetoid sensilla; cos – coeloconic sensilla; bcs – basiconic sensilla; cfs – campaniform sensilla; ant – anterior direction; dor – dorsal direction; lat – lateral direction. Hidden part of the mandible, not visible from the outside, is shown in gray.

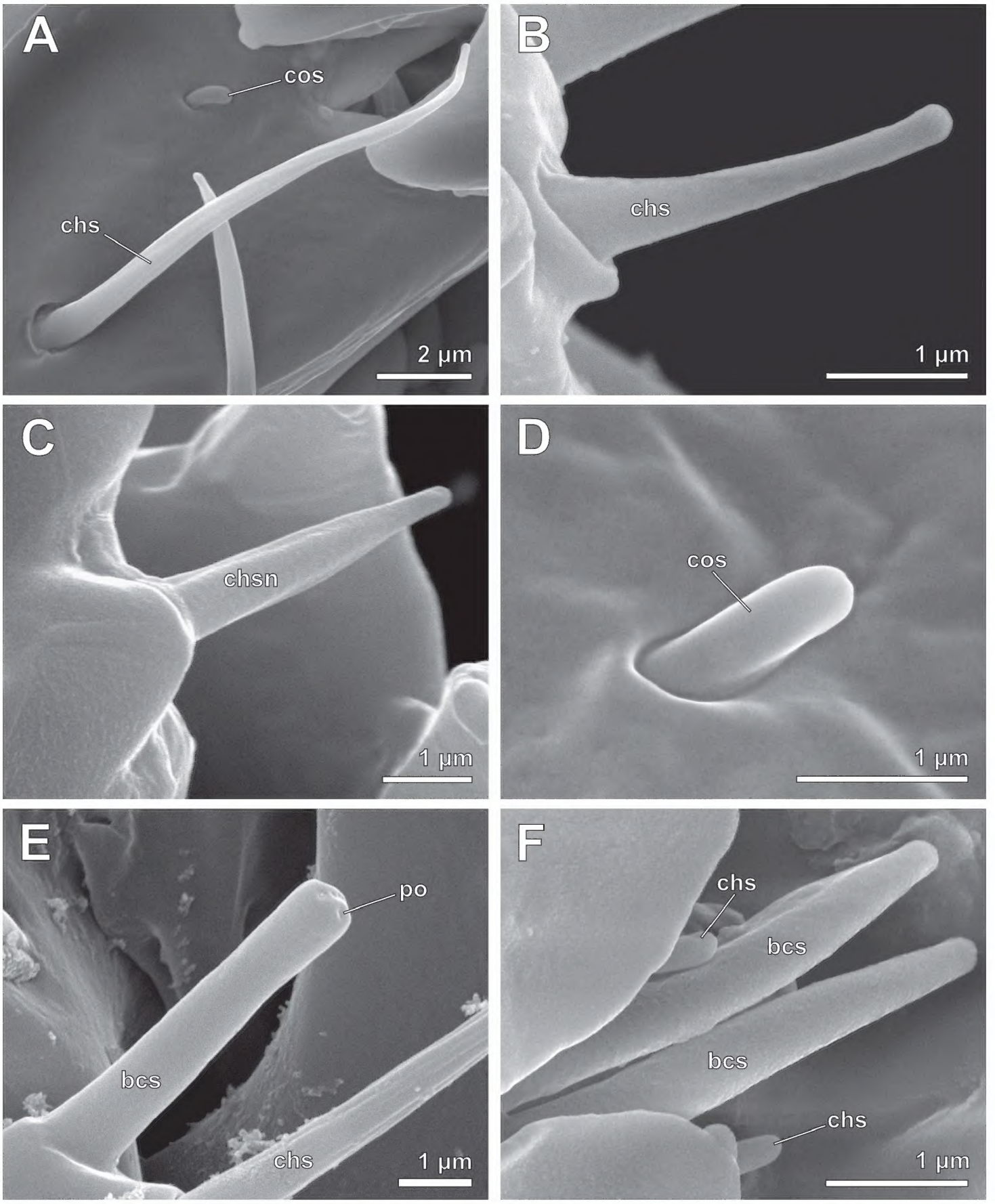

Figure 3. Types of sensilla on *M. viggianii* mouthparts. **A** chaetoid sensillum on lateral surface of mandible **B** chaetoid sensillum on labial palp **C** non-innervated chaetoid sensillum on the distal part of maxilla **D** coeloconic sensillum on lateral surface of mandible **E** porous basiconic sensillum on maxillary palp **F** aporous basiconic and chaetoid sensilla on distal part of labium. Abbreviations: chs – chaetoid sensilla; chsn – non-innervated chaetoid sensilla; cos – coeloconic sensilla; bcs – basiconic sensilla; po – pores.

other three chaetoid sensilla on the medial surface are located close to each other near the distal part of the mandible and not are visible from the outside. Coeloconic sensilla are positioned on the lateral surface of the mandible. There is one coeloconic sensillum

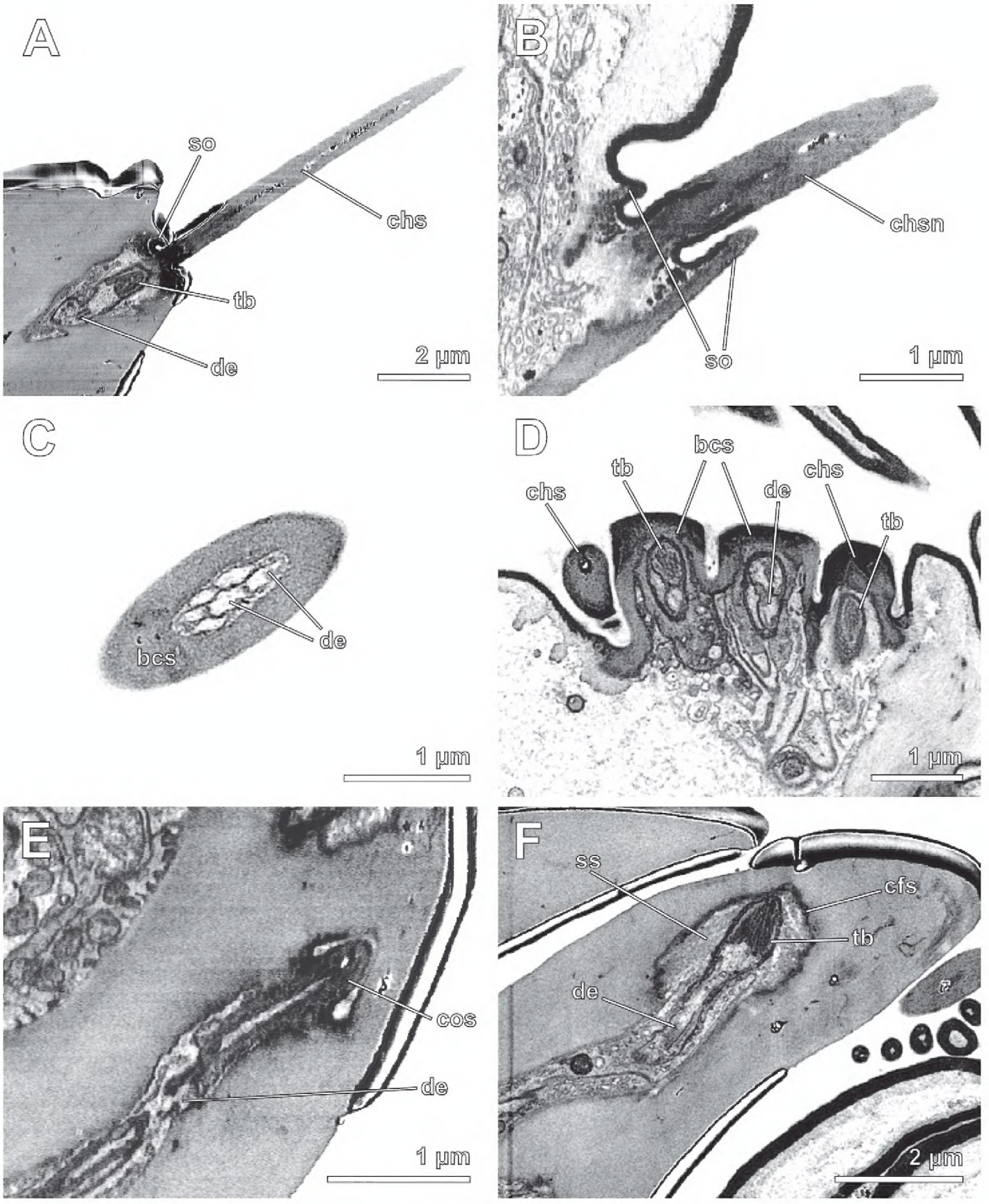

Figure 4. Ultrastructure of sensilla on *M. viggianii* mouthparts. **A** chaetoid sensillum on mandible **B** non-innervated chaetoid sensillum on maxilla **C** basiconic sensillum on maxillary palp, cross-section **D** basiconic and chaetoid sensilla on tip of labium, cross-section of the base **E** coeloconic sensillum on mandible **F** campaniform sensillum on mandible. Abbreviations: chs – chaetoid sensilla; chsn – non-innervated chaetoid sensilla; bcs – basiconic sensilla; cos – coeloconic sensilla; cfs – campaniform sensilla; so – socket; tb – tubular body; de – dendrite; ss – socket septum.

in the proximal part and one on the distal part of the mandible. Each mandible also bears 10 campaniform sensilla distributed from the base to the tip. The sensilla occur on both the medial and lateral surfaces.

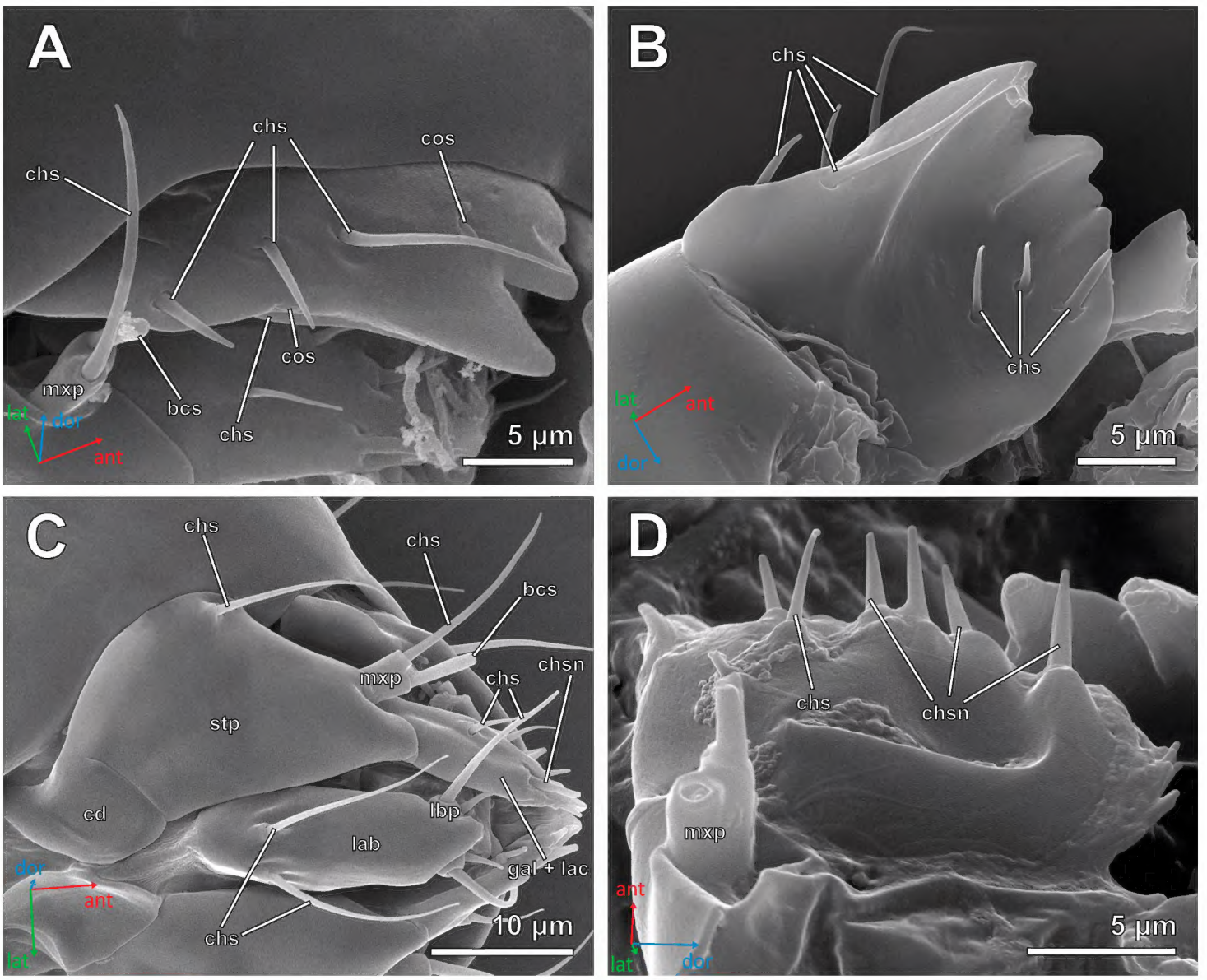

Figure 5. Mandible (**A, B**) and maxilla (**C, D**) of *M. viggianii*. **A** lateral surface of mandible **B** medial surface of mandible **C** ventral surface of maxilla **D** dorsal surface of maxilla. Abbreviations: mxp – maxillary palp; cd – cardo; stp – stipes; gal – galea; lac – lacinia; lab – labia; lbp – labial palp; chs – chaetoid sensilla; chsn – non-innervated chaetoid sensilla; cos – coeloconic sensilla; bcs – basiconic sensilla; ant – anterior direction; dor – dorsal direction; lat – lateral direction.

A maxilla (Figs 2C, D, 5C, D) consists of the cardo, stipes, merged galea and lacinia, and one-segmented maxillary palp. The only sensillum on the stipes is a chaetoid one on its lateral surface. The maxillary palp has two sensilla: chaetoid and porous basiconic (Fig. 6A). The galea has two innervated chaetoid sensilla on its lateral surface and six non-innervated chaetoid sensilla on its tip. These are pointing distally.

The labium (Fig. 2E) has the smallest number of sensilla. It consists of the prementum and postmentum, the latter consisting of the mentum and submentum. The submentum bears no sensilla. The base of the mentum bears two chaetoid sensilla pointing distally and laterally. The mentum also bears a pair of one-segmented labial palp located on its distal part and bearing two chaetoid sensilla that differ drastically in length (Fig. 6B). The prementum, the apical part of the labium, has a group of four sensilla: two chaetoid sensilla located laterally and two aporous basiconic sensilla located medially. These four sensilla are likely positioned on the reduced glossae and paraglossae.

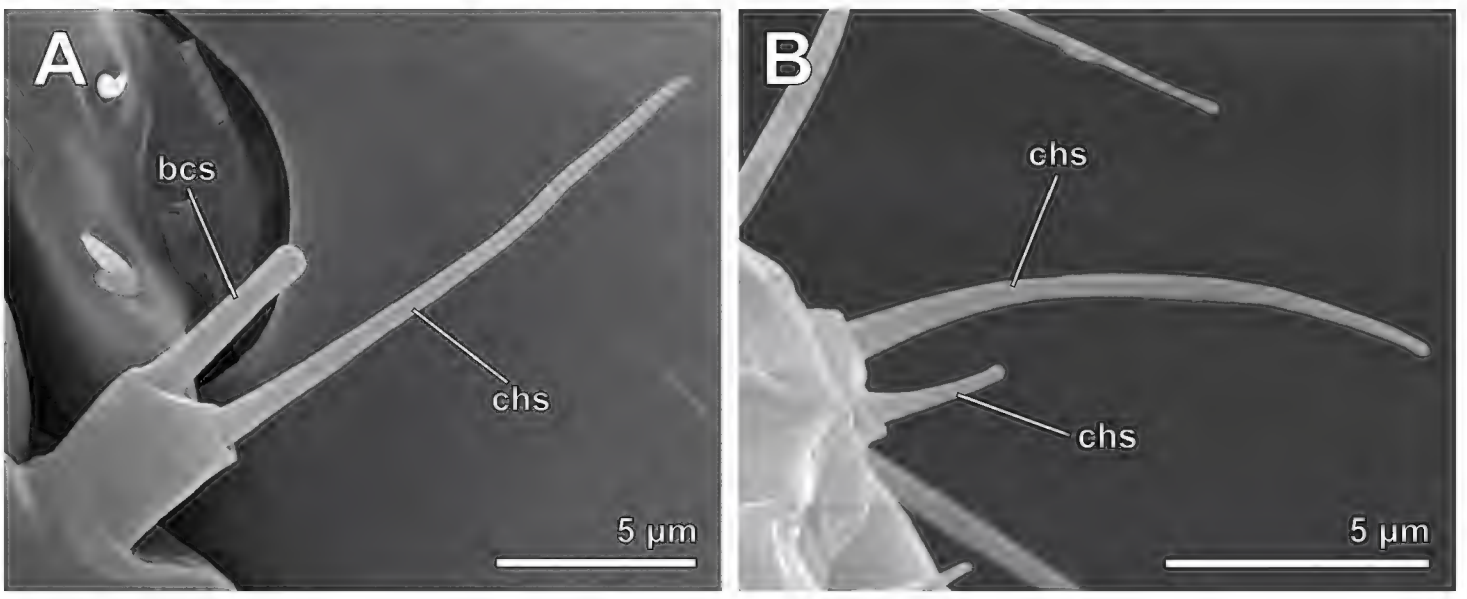

Figure 6. Maxillary (**A**) and labial (**B**) palps of *M. viggianii*. Abbreviations: chs – chaetoid sensilla; bcs – basiconic sensilla.

Aberrations in the set of sensilla

Some of the studied specimens lack one or two of the sensilla in random positions. One of the studied males lacks the shorter chaetoid sensillum (lbp-chs-2) on its right labial palp. Another male does not have one of the chaetoid sensilla (md-chs-2) on the lateral surface of its right mandible. One of the studied females has two aberrations at the same time: it lacks one chaetoid sensillum on the lateral surface of the right mandible (md-chs-4) and has a single chaetoid sensillum positioned in the middle of the base of the labium instead of a pair of such sensilla (lab-chs-1).

Discussion

Structure and possible functions of the sensilla

The majority of sensilla on the mouthparts of *M. viggianii* appear to be mechanoreceptors. Chaetoid sensilla are the most common (aporous sensilla according to classification by Altner and Prillinger 1980). Their elongated shape, aporous surface, basal socket, and well-developed tubular body at the base suggest the mechanosensory function. The chaetoid sensilla have only one dendrite, which means most likely that they have no additional functions. The mechanosensory function of chaetoid sensilla was previously described by Wolbarsht (1960) who measured with electrodes their electrophysiological responses to inclining. Chaetoid sensilla on the distal parts of maxillae are not innervated and thus do not possess sensory functions. Considering that they have a stout shape and are located exclusively on the distal parts of maxilla, they may be used for mechanical food processing.

Like in most chaetoid sensilla, the tubular body is present in campaniform sensilla (aporous sensilla by Altner and Prillinger 1980), which are also most likely mechanore-

ceptors. They respond electrophysiologically to cuticle deformations, and thus are mechanoreceptors, as shown in leg movements e. g., Delcomyn 1990). Campaniform sensilla of *M. viggianii* are completely hidden under the cuticle and may be proprioceptors, perceiving deformations, which may be important in mandibles. These sensilla show significant structural reductions: unlike sensilla of the same type in other studied insects (Moran and Rowley 1975; Müller et al. 1978; Saltin et al. 2023), they have no cuticular dome or sensillar cavity. The cuticle of *M. viggianii* may be thin enough to allow perception of its deformation by campaniform sensilla without a cuticular dome of thinner cuticle.

One of the three dendrites of aporous basiconic sensilla (aporous sensilla by Altner and Prillinger 1980) on the labium also has a tubular body, which suggests that these sensilla have a mechanosensory function but also possess other modalities. These might be chemosensory or thermo-hygrosensory. Basiconic sensilla on the maxillary palps bear pores (multiporous sensilla by Altner and Prillinger 1980), contain six dendrites, and have a thick cuticle, so they may be contact chemoreceptors responding to various chemical compounds. Basiconic sensilla in insects often have a chemosensory function, e.g., it was shown using the single sensillum recording method that in locusts they respond to chemical odorants (Li et al. 2018).

Coeloconic sensilla (aporous sensilla by Altner and Prillinger 1980) on the mandible have one dendrite without a tubular body and thus do not possess a mechanosensory function. They also have no pores, which makes them unlikely to be chemoreceptors. They may be thermo- or hygroreceptors, which is common for coeloconic sensilla (Chapman 1969). Their function has been described in Schneider et al. (2018); in that electrophysiological study, it was established that coeloconic sensilla of the katydid *Mecopoda* Serville respond to temperature and/or humidity.

The absence of auxiliary cells (thecogen, tormogen, or trichogen) in the mouthpart sensilla is a distinctive feature likely resulting from the extreme miniaturization of *M. viggianii*. This has been previously observed in the placoid sensilla on antennae of *M. viggianii* (Diakova and Polilov 2021). Given that auxiliary cells play critical roles – such as providing structural support, nourishment, and secretion of the sensillum cuticle – it is plausible that their loss occurs after the sensillum has been formed. This type of cellular reductions in sensilla has not been reported before and requires further in-depth investigation of pupal sensilla to understand the developmental stages of these structures.

Sexual dimorphism and stability of sensilla set

The structure, diversity, and distribution of sensilla on the mouthparts show no sexual dimorphism. The sizes of the sensilla show no significant differences between males and females (one-way Kruskal–Wallis ANOVA test, $p > 0.05$). In contrast, the antennal sensilla of *M. viggianii* show sexual dimorphism: female antennae bear more sensilla than in male and have aporous placoid and basiconic sensilla, which are absent in males (Diakova et al. 2018). Likely, the antenna of *M. viggianii* has sex-specific functions, e.g., male-female interactions and host location, while mouthparts only have

sex-independent functions, e.g., food processing, which leads to the absence of sexual differences. The set of sensilla on mouthparts of *M. viggianii* is generally identical in different individuals. Aberrations occur rarely and randomly, suggesting that these are developmental deviations.

Comparison with other Hymenoptera

The diversity of mouthpart sensilla in other Hymenoptera is very similar to that of *M. viggianii*: they always have chaetoid sensilla present on all mouthparts; trichoid and basiconic sensilla also commonly occur (Whitehead and Larsen 1976; Navasero and Elzen 1991; Barsagade et al. 2010, 2017; Zhang et al. 2012, 2015; Kumar and Kumar 2015; Baranek Bianca et al. 2018; Wu et al. 2018; Hamdy and Emam 2022; Tan et al. 2025). Some representatives also have campaniform sensilla (Baranek Bianca et al. 2018; Hamdy and Emam 2022). Comparison of the nomenclature used for sensilla in different studies is given in Suppl. material 1: table S3.

Unfortunately, only one of previous studies on Hymenoptera provides data on ultrastructure of mouthpart sensilla (Whitehead and Larsen 1976), other studies provide only scanning electron micrographs. That study revealed that *A. mellifera* L. has five dendrites and auxiliary cells in chaetoid sensilla, unlike *M. viggianii*, which has only a single dendrite in each chaetoid sensillum and no auxiliary cells. By contrast, the ultrastructure of sensilla on the glossal tip in *A. mellifera* is quite similar to that of *M. viggianii*: it has five dendrites one of which contains a tubular body and hence has a mechanosensory function, while the others have other functions. While Whitehead and Larsen (1976) provided some data on ultrastructure of the sensilla, scarce data makes it difficult to speculate about the functions of some mouthpart sensilla in the previously studied Hymenoptera and to compare them to those of *M. viggianii*.

Males of another parasitic wasp *Dicopomorpha echmepterygis* Mockford are even smaller than *Megaphragma*. Their body length is 0.14 to 0.24 mm, they are blind and wingless, have strongly reduced leg structures, possess only one antennal segment and lack mouthparts (Mockford 1997; Huber et al. 2020; Boudinot et al. 2021b). Apparently, they have a very short lifespan which is enough to transfer the gametes to a female, and thus complex sensory structures are not needed. This leads to a major loss of sensory organs and functions in *D. echmepterygis* males, making them less informative objects for studying sensory system scaling in insects.

Another miniature parasitic wasp, *Trichogramma dendrolimi* Matsumura has approximately 80 sensilla on its mouthparts (Zhang et al. 2012), slightly more than in *M. viggianii* (about 70 sensilla in total). The location of sensilla in *T. dendrolimi* is similar to that of *M. viggianii*, e.g., chaetoid sensilla occur in *T. dendrolimi* on all mouthparts and are the most common type of sensilla there; they also are positioned very similarly to the mouthpart sensilla of *M. viggianii*. Each maxillary palp of *T. dendrolimi* bears an elongated sensillum with multiple pores on its surface; this sensillum is most likely homologous to the porous basiconic sensilla of *M. viggianii*. The mouthparts of *T. dendrolimi* showed no sexual dimorphism, as in *M. viggianii*.

Larger parasitoid wasps, *Telenomus dendrolimusi* Chu (Zhang et al. 2015), *Leptocybe invasa* Fisher and LaSalle, *Ophelimus maskelli* (Hamdy and Emam 2022), *Aphidius gifuensis* Ashmead (Wu et al. 2018), *Microplitis croceipes* (Cresson) (Navasero and Elzen 1991), and *Eurytoma plotnikovi* Nikolskaya (Tan et al. 2025) share a similar pattern: the majority of sensilla on their mouthparts are chaetoid. *L. invasa* and *O. maskelli* also have campaniform sensilla on their mandibles (similar to *M. viggianii*), coeloconic sensilla on their maxillae and basiconic sensilla on their maxillary and labial palps. Campaniform sensilla of *L. invasa* and *O. maskelli* have a developed cuticular part and thus can be visible from the cuticular surface unlike campaniform sensilla in *M. viggianii*. To sum up, the diversity of mouthpart sensilla in these parasitoids is similar to that of *M. viggianii*.

The number of mouthpart sensilla in these parasitoid wasps is generally slightly greater than in *M. viggianii* and depends on their body length: the smaller (0.7–1.5 mm) *T. dendrolimusi*, *L. invasa*, and *O. maskelli* have 85–110 sensilla on their mouthparts, while the larger (1.8–3 mm) *A. gifuensis* has approximately 250–300 sensilla. Despite being 3–5 mm long, *E. plotnikovi* has a relatively small number of mouthpart sensilla, 100–150. Like *M. viggianii*, the larger parasitoid wasps *T. dendrolimusi* and *A. gifuensis* do not show sexual dimorphism in structure or distribution of their mouthpart sensilla. By contrast, *E. plotnikovi* shows sexual dimorphism in sensilla size: its chaetoid and trichoid sensilla are generally longer in males. Only females were studied in *L. invasa* and *O. maskelli*, so there is no data on the sexual dimorphism in their mouthpart sensilla.

The diversity of sensilla in social Hymenoptera is very similar to that of parasitoid wasps. They possess numerous chaetoid sensilla on all their mouthparts; trichoid sensilla are also very common (Whitehead and Larsen 1976; Barsagade et al. 2010; Kumar and Kumar 2015; Barsagade et al. 2017; Baranek Bianca et al. 2018; Boudinot et al. 2021a). *Vespula germanica* (Fabricius) and *Vespula vulgaris* L. also have campaniform sensilla on their mandibles and galeae (Baranek Bianca et al. 2018). These are visible from the outside, unlike those of *M. viggianii*. Basiconic sensilla commonly occur in social hymenopterans on mandibles, galeae, glossae, and labial palps. These basiconic sensilla do not have pores, unlike the sensilla of the same type located on the maxillary palps in *M. viggianii*. Maxillary palps of the ant *Dorylus helvolus* L. also posess a small group of peculiar hemispherical or papilla-like sensilla (Boudinot et al. 2021a).

The number of sensilla is the greatest in *V. germanica* and *V. vulgaris*: they have several thousand sensilla on their mouthparts. Despite having almost the same body size, *A. mellifera* has a total of 190–235 mouthpart sensilla (Whitehead and Larsen 1976). The ant *Leptogenys dentilobis* Forel has a similar number of mouthpart sensilla, 200–300 (Barsagade et al. 2017). As could be expected, social hymenopterans show sexual dimorphism. Females of *V. germanica* and *V. vulgaris* have smaller total numbers of mouthpart sensilla (Baranek Bianca et al. 2018). Females (both gynes and workers) of the ant *Camponotus compressus* (Fabricius) have basiconic sensilla, while males lack them (Barsagade et al. 2010). Only worker females were studied for *A. mellifera*, *A. florea*, and *L. dentilobis*, so there is no data about the sexual dimorphism of their mouthpart sensilla (Whitehead and Larsen 1976; Kumar and Kumar 2015; Barsagade et al. 2017).

Conclusion

We show that despite extreme miniaturization, *M. viggianii* maintains a diverse set of mouthpart sensillum types, comparable to those found in larger hymenopterans. However, most of these sensilla exhibit notable structural simplifications, particularly the absence of auxiliary cells. The general number of sensilla shows a tendency to decrease along with the body size, but even the minute *M. viggianii* retains 70 sensilla on its mouthparts. All these effects correspond to results of previous studies (Makarova et al. 2022b). The predominance of mechanosensory structures, especially chaetoid and campaniform sensilla, suggests a primarily tactile function, while specific basiconic and coeloconic sensilla may have additional roles in chemoreception or thermo- and hygroreception. Importantly, the lack of sexual dimorphism in mouthpart sensilla contrasts with the clear differences observed in antennal sensilla, underscoring a functional divergence likely linked to sex-specific behaviors.

Our findings highlight the evolutionary retention of sensory diversity and function in the mouthparts of miniature parasitoid wasps, while also emphasizing the modifications imposed by miniaturization. Given the scarcity of detailed ultrastructural data for mouthpart sensilla in other Hymenoptera, our results serve as an important reference point for future comparative studies of the scaling of sensory system in insects.

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References

Altner H, Prillinger L (1980) Ultrastructure of invertebrate chemo-, thermo-, and hygroreceptors and its functional significance. International Review of cytology 67: 69–139. https://doi.org/10.1016/S0074-7696(08)62427-4

Bernardo U, Viggiani G (2002) Biological data on *Megaphragma amalphitanum* Viggiani and *Megaphragma mymaripenne* Timberlake (Hymenoptera: Trichogrammatidae), egg-parasitoid of *H. haemorrhoidalis* (Bouch?) (Thysanoptera: Thripidae) in southern Italy. Bollettino del Laboratorio di Entomologia Agraria Filippo Silvestri 58: 77–85.

Boudinot BE, Moosdorf OTD, Beutel RG, Richter A (2021a) Anatomy and evolution of the head of *Dorylus helvolus* (Formicidae: Dorylinae): Patterns of sex-and caste-limited traits in the sausagefly and the driver ant. Journal of Morphology 282(11): 1616–1658. https://doi.org/10.1002/jmor.21410

Boudinot BE, Beutel RG, Gorb SN, Polilov AA (2021b) Functional diversity of attachment and grooming leg structures is retained in all but the smallest insects. Journal of Zoology 313(2). https://doi.org/10.1111/jzo.12840

Chapman RF (1969) The Insects. Structure and Function. Hodder and Stoughton, London, 819 pp.

Chua NJ, Makarova AA, Gunn P, Villani S, Cohen B, Thasin M, Wu J, Shefter D, Pang S, Shan Xu C, Hess HF, Polilov AA, Chklovskii DB (2023) A complete reconstruction of the early visual system of an adult insect. Current Biology 33(21): 4611–4623. https://doi.org/10.1016/j.cub.2023.09.021

Das P, Chen L, Sharma KR, Fadamiro HY (2011) Abundance of antennal chemosensilla in two parasitoid wasps with different degree of host specificity may explain sexual and species differences in their response to host-related volatiles. Microscopy Research and Technique 74: 900–909. https://doi.org/10.1002/jemt.20974

Delcomyn F (1991) Activity and directional sensitivity of leg campaniform sensilla in a stick insect. Journal of comparative physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology 168(1): 113–119. https://doi.org/10.1007/BF00217109

Desyatirkina IA, Makarova AA, Pang S, Xu CS, Hess H, Polilov AA (2023) Multiscale head anatomy of *Megaphragma* (Hymenoptera: Trichogrammatidae). Arthropod Structure & Development 76: e101299. https://doi.org/10.1016/j.asd.2023.101299

Diakova AV, Makarova AA, Polilov AA (2018) Between extreme simplification and ideal optimization: antennal sensilla morphology of miniaturized *Megaphragma* wasps (Hymenoptera: Trichogrammatidae). PeerJ 6. https://doi.org/10.7717/peerj.6005

Diakova AV, Polilov AA (2020) Sensation of the tiniest kind: the antennal sensilla of the smallest free-living insect *Scydosella musawasensis* (Coleoptera: Ptiliidae). PeerJ 8. https://doi.org/10.7717/peerj.10401

Diakova AV, Polilov AA (2021) Porous or non-porous? The challenge of studying unusual placoid sensilla of *Megaphragma* wasps (Hymenoptera, Trichogrammatidae) with electron microscopy. Journal of Hymenoptera Research 84: 69–73. https://doi.org/10.3897/jhr.84.68707

Fischer S, Müller CHG, Meyer-Rochow VB (2011) How small can small be: The compound eye of the parasitoid wasp *Trichogramma evanescens* (Westwood, 1833) (Hymenoptera, Hexapoda), an insect of 0.3- to 0.4-mm total body size. Visual Neuroscience 28(4): 295–308. https://doi.org/10.1017/S0952523810000192

Fischer S, Lu Z, Meinertzhagen IA (2019) Three-dimensional ultrastructural organization of the ommatidium of the minute parasitoid wasp *Trichogramma evanescens*. Arthropod Structure & Development 48: 35–48. https://doi.org/10.1016/j.asd.2018.12.003

Godfrey RK, Oberski JT, Allmark T, Givens C, Hernandez-Rivera J, Gronenberg W (2021) Olfactory system morphology suggests colony size drives trait evolution in odorous ants (Formicidae: Dolichoderinae). Frontiers in Ecology and Evolution 9: e733023. https://doi.org/10.3389/fevo.2021.733023

Gokan N, Meyer-Rochow VB (2000) Morphological comparisons of compound eyes in Scarabaeoidea (Coleoptera) related to the beetles' daily activity maxima and phylogenetic positions. Journal of Agricultural Science 45: 15–61.

Hallberg E, Hansson BS (1999) Arthropod sensilla: morphology and phylogenetic considerations. Microscopy research and Technique 47(6): 428–439. https://doi.org/10.1002/(SICI)1097-0029(19991215)47:6<428::AID-JEMT6>3.3.CO;2-G

Honkanen A, Meyer-Rochow VB (2009) The eye of the parthenogenetic and minute moth *Ectoedemia argyropeza* (Lepidoptera: Nepticulidae). European Journal of Entomology 106: 619–629. https://doi.org/10.14411/eje.2009.078

Huber JT, Read JD, Triapitsyn SV (2020) Illustrated key to genera and catalogue of Mymaridae (Hymenoptera) in America north of Mexico. Zootaxa 4773(1): 1–411. https://doi.org/10.11646/zootaxa.4773.1.1

Ivanov VP (2000) Sensory Organs of Insects and Other Arthropods. Nauka, Moscow, 279 pp. [in Russian]

Kamikouchi A, Inagaki HK, Effertz T, Hendrich O, Fiala A, Göpfert MC, Ito K (2009) The neural basis of *Drosophila* gravity-sensing and hearing. Nature 458(7235): 165–171. https://doi.org/10.1038/nature07810

van der Kooi CJ, Stavenga DG, Arikawa K, Belušič G, Kelber A (2021) Evolution of insect color vision: from spectral sensitivity to visual ecology. Annual review of entomology 66(1): 435–461. https://doi.org/10.1146/annurev-ento-061720-071644

Li H, You Y, Zhang L (2018) Single sensillum recordings for locust palp sensilla basiconica. Journal of Visualized Experiments: JoVE (136): e57863. https://doi.org/10.3791/57863

Makarova AA, Polilov AA, Fischer S (2015) Comparative morphological analysis of compound eye miniaturization in minute Hymenoptera. Arthropod Structure & Development. 44: 21–32. https://doi.org/10.1016/j.asd.2014.11.001

Makarova AA, Meyer-Rochow VB, Polilov AA (2019) Morphology and scaling of compound eyes in the smallest beetles (Coleoptera: Ptiliidae). Arthropod Structure & Development 48: 83–97. https://doi.org/10.1016/j.asd.2019.01.001

Makarova AA, Diakova AA, Chaika SY, Polilov AA (2022a) Scaling of the sense organs of insects. 1. Introduction. Compound eyes. Entomological Review 102(2): 161–181. https://doi.org/10.1134/S0013873822020026

Makarova AA, Diakova AA, Chaika SY, Polilov AA (2022b) Scaling of the sense organs of insects. 2. Sensilla. Discussion. Conclusion. Entomological Review 102(3): 323–346. https://doi.org/10.1134/S0013873822030058

Makarova AA, Chua NJ, Diakova AV, Desyatirkina IA, Gunn P, Pang S, Xu CS, Hess HF, Chklovskii DB, Polilov AA (2025) The first complete 3D reconstruction and morphofunctional mapping of an insect eye. eLife 14: RP103247. https://doi.org/10.7554/eLife.103247.2

Mazokhin-Porshnyakov GA, Elizarov YA, Zhantiev RD, Tshernyshev WB (1983) A Guide to the Physiology of Insect Senses. Moscow State University, 262 pp. [in Russian]

Meyer-Rochow VB, Gál J (2004) Dimensional limits for arthropod eyes with superposition optics. Vision Research 44: 2213–2223. https://doi.org/10.1016/j.visres.2004.04.009

Meyer-Rochow VB (2014) Compound eyes of insects and crustaceans: Some examples that show there is still a lot of work left to be done. Insect Science 22: 461–481. https://doi.org/10.1111/1744-7917.12117

Minelli A, Fusco G (2019) No limits: Breaking constraints in insect miniaturization. Arthropod Structure & Development 48: 4–11. https://doi.org/10.1016/j.asd.2018.11.009

Missbach C, Dweck HK, Vogel H, Vilcinskas A, Stensmyr MC, Hansson BS, Grosse-Wilde E (2014) Evolution of insect olfactory receptors. eLife 3: e02115. https://doi.org/10.7554/eLife.02115

Mockford EL (1997) A new species of *Dicopomorpha* (Hymenoptera: Mymaridae) with diminutive, apterous males. Annals of the Entomological Society of America 90(2): 115–120. https://doi.org/10.1093/aesa/90.2.115

Moran DT, Rowley JC (1975) High voltage and scanning electron microscopy of the site of stimulus reception of an insect mechanoreceptor. Journal of ultrastructure research 50(1): 38–46. https://doi.org/10.1016/S0022-5320(75)90006-4

Müller ML, Honegger HW, Nickel E, Westphal C (1978) The ultrastructure of campaniform sensilla on the eye of the cricket, *Gryllus campestris*. Cell and Tissue Research 195: 349–357. https://doi.org/10.1007/BF00236731

Navasero RC, Elzen GW (1991) Sensilla on the antennae, foretarsi and palpi of *Microplitis croceipes* (Cresson) (Hymenoptera: Braconidae). Proc Entomol Soc Washington 93: 343–347.

Saltin BD, Haustein M, Büschges A, Blanke A (2023) A parametric finite element model of leg campaniform sensilla in *Drosophila* to study CS location and arrangement. bioRxiv 2023-07. https://doi.org/10.1101/2023.07.24.550300

Schneider ES, Kleineidam CJ, Leitinger G, Römer H (2018) Ultrastructure and electrophysiology of thermosensitive sensilla coeloconica in a tropical katydid of the genus *Mecopoda* (Orthoptera, Tettigoniidae). Arthropod Structure & Development 47(5): 482–497. https://doi.org/10.1016/j.asd.2018.08.002

Slifer EH (1970) The structure of arthropod chemoreceptors. Annual review of entomology. 15(1): 121–142. https://doi.org/10.1146/annurev.en.15.010170.001005

Smallegange RC, Kelling FJ, Otter CJD (2008) Types and numbers of sensilla on antennae and maxillary palps of small and large houseflies, *Musca domestica* (Diptera, Muscidae). Microscopy research and technique 71(12): 880–886. https://doi.org/10.1002/jemt.20636

Symonds MR, Elgar MA (2013) The evolution of body size, antennal size and host use in parasitoid wasps (Hymenoptera: Chalcidoidea): a phylogenetic comparative analysis. PLoS ONE 8(10): e78297. https://doi.org/10.1371/journal.pone.0078297

Snodgrass RE (1926) The morphology of insect sense organs and the sensory nervous system. Smithsonian Miscellaneous Collections.

Polilov AA (2012) The smallest insects evolve anucleate neurons. Arthropod Structure & Development 41(1): 29–34. https://doi.org/10.1016/j.asd.2011.09.001

Polilov AA (2015) Small Is Beautiful: Features of the Smallest Insects and Limits to Miniaturization. Annual Review of Entomology 60: 103–121. https://doi.org/10.1146/annurev-ento-010814-020924

Polilov AA (2016) At the Size Limit – Effects of Miniaturization in Insects. Springer International Publishing, 325 pp. https://doi.org/10.1007/978-3-319-39499-2

Polilov AA (2017) Anatomy of adult *Megaphragma* (Hymenoptera: Trichogrammatidae), one of the smallest insects, and new insight into insect miniaturization. PLoS ONE 12(5): e0175566. https://doi.org/10.1371/journal.pone.0175566

Polilov AA, Hakimi KD, Makarova AA (2023) Extremely small wasps independently lost the nuclei in the brain neurons of at least two lineages. Scientific Reports 13(1): e4320. https://doi.org/10.1038/s41598-023-31529-4

Wolbarsht ML (1960) Electrical characteristics of insect mechanoreceptors. The Journal of general physiology 44(1): 105–122. https://doi.org/10.1085/jgp.44.1.105

van der Woude E, Smid HM (2016) How to escape from Haller's rule: olfactory system complexity in small and large *Trichogramma evanescens* parasitic wasps. Journal of Comparative Neurology 524(9): 1876–1891. https://doi.org/10.1002/cne.23927

Zacharuk RY, Shields VD (1991) Sensilla of immature insects. Annual Review of Entomology 36: 331–354. https://doi.org/10.1146/annurev.en.36.010191.001555

Supplementary material 1

Types of mouthpart sensilla in different Hymenoptera

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Data type: docx

Explanation note: **table S3.** (supplementary) Abbreviations: chs – chaetoid sensilla; chsn – non-innervated chaetoid sensilla; cfs – campaniform sensilla; bcs – basiconic sensilla; cos – coeloconic sensilla; mxp – maxillary palp; lbp – labial palp.

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